A new subspecies of the freshwater halacarid mite *Lobohalacarus weberi* (Romijn and Viets) (Halacaridae, Acari) from a Southern Atlantic Ocean island

by

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ABSTRACT

Lobohalacarus weberi tristanensis subsp. nov., found on Inaccessible, Tristan da Cunha Islands, is described and compared with populations of *L. weberi weberi* (Romijn and Viets) from Europe. Representatives of the Lobohalacarus weberi complex primarily inhabit subterranean waters. A short survey of species and subspecies of the *L. weberi* complex is given and means of dispersal to Inaccessible Island are discussed.

INTRODUCTION

Although comprising mostly marine species, the superfamily Halacaroidea includes several fresh water species. At present, about 700 marine and 50 limnic species are described. The freshwater halacarid species differ from marine species in having external genital acetabula. The freshwater species can be assigned to several halacarid subfamilies.

AREA OF INVESTIGATION, MATERIAL AND ABBREVIATIONS

The Tristan da Cunha island group lies about midway between South Africa and South America, in a belt with prevailing westerly winds and easterly water currents (Baker *et al.*, 1964). The islands, of volcanic origin, are located east of the mid-Atlantic Ridge. Inaccessible, the most westerly island, has an area of about 10 km and reaches a height of 550 m (Baker, 1973). The island is resting on an older eroded volcanic cone, about 18 million years old (Baker *et al.*, 1964; Chevallier *et al.*, 1992).

The halacarid specimens were collected on the west side of Inaccessible Island, from a small, narrow freshwater stream bordered by *Spartina arundinacea*. The sampling site is less than 1 km from the underground source of the stream; the water is clear, pH 7.0 (Barber-James, in prep).

Abbreviations used in the descriptions are: AD, anterior dorsal plate; AE, anterior epimeral plate; br, bristle; GA, genitoanal plate; GO, genital opening; OC, ocular plate(s); P, palp, P-2, 2nd palpal segment; pas, parambulacral setae; PD, posterior dorsal plate; PE, posterior epimeral plate; sp, spine. Legs are numbered I to IV, leg segments 1 to 6 (I-1, I-2, I-3, I-4, I-5, I-6 = trochanter, basifemur, telofemur, genu, tibia and tarsus on leg I).

The type material is deposited in the Albany Museum, Grahamstown, South Africa.

TAXONOMY

Lobohalacarus weberi tristanensis subsp. nov.

MATERIAL

One holotype female, Albany Museum, Grahamstown, TDC II H; Inaccessible Island, from

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narrow freshwater stream; collected by H.M. Barber-James, 23 October 1989.

Three paratype females, one larva, Albany Museum, Grahamstown, TDC I G; type locality. Two females, author's halacarid collection, type locality.

DESCRIPTION

Holotype female. Idiosoma 310 μ m long. Integument of dorsal plates foveate and delicately punctate. Anterior rounded idiosoma formed by dorsal portion of AE which is fused in midline. Anterior AD contiguous but not broadly joined with that area. AD 92 μ m long; with an area like an inverted Y slightly raised (Fig. 1). AD with 18-20 foveae in width and 17 foveae in length. OC elongate, 75 μ m long; no cornea present. PD 184 μ m long, with two slightly raised longitudinal costae; transversely about 20-22 foveae wide, longitudinally with 27-29 foveae. Dorsal idiosomatic setae small; one pair of setae inserted anterior to the AD, one pair on the AD on a level with insertion of leg I, one pair each in anterolateral edge and near medial edge of OC. PD with three pairs of setae, one of them on a level with insertion of leg III, one on that of leg IV, and one pair of setae in posterior PD.

Ventral shield (fused anterior epimeral plate, posterior epimeral plate and genitoanal plate) delicately foveate and punctate. Area corresponding to AE with three pairs of long ventral setae and one pair of epimeral pores (Fig. 2); area of PE with one dorsal, one long lateral and one ventral seta. GO 70 μ m long; genital sclerites with two pairs of acetabula. These acetabula in size and morphology similar to epimeral pores. Area of GA with two and four perigenital setae (asymmetrically). Ovipositor short, in rest hardly extending beyond the GO.

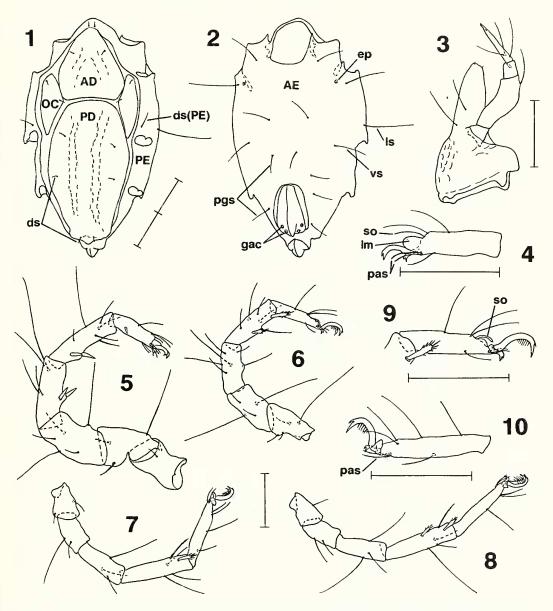
Gnathosoma 108 μ m long, with rostrum and gnathosoma base similar in length. Both pairs of maxillary setae inserted near the rostral base. Palps 4-segmented; P-2 with one long dorsal seta; P-3 with medial spine; P-4 with three basal setae (Fig. 3).

Leg I stouter than posterior legs. All legs with basifemora and telofemora subequal in length. Genu I slightly longer than telofemur I (Fig. 5), II-4 slightly shorter than II-3 (Fig. 6), and genua on legs III and IV longer than telofemora, respectively (Figs 7 and 8). All tibiae longer than genua. Number of setae, from trochanter to tarsus (pas and solenidion included): leg I, 1, 3, 5, 6, 8, 11; leg II, 1, 4, 4, 6, 7, 7; leg III, 1, 2, 2, 3, 5, 6; leg IV, 0, 1, 2, 3, 6, 5. Genu I ventrally with two short spines, I-5 with basal pair of short spines and distal pair of bristles. Tibiae II and IV with one slender ventral bristle and two short and pectinate bristles; tibia III with one seta and one pectinate bristle. Tarsus I with one ventromedial spine, two short ventral setae and three long dorsal setae, tip of tarsus with seta-like dorsolateral solenidion, conspicuously large lateral membrane (Fig. 4) and doubled lateral and medial pas. Solenidion on tarsus II hollow, dorsomedial in position (Fig. 9). Number of dorsal/ventral setae on tarsi II to IV: 3/1, 3-4/0-1 (asymmetrically), 3/0; posterior tarsi with a pair of single pas.

Pair of claws on tarsus I smaller than on posterior tarsi; claws with accessory process but without long pecten. Claws on tarsi II to IV with pectens bearing long tines.

Male. Unknown.

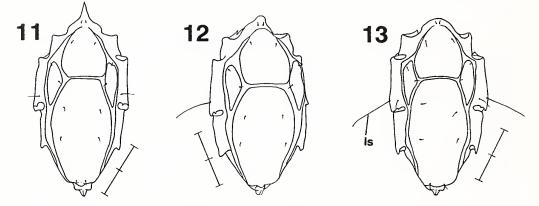
Juveniles. Deutonymph and protonymph unknown. Larva 185 µm long. Dorsal plates foveate. Anterior margin of idiosoma truncate. Number of dorsal setae same as in adults but first pair of setae in anterior margin of idiosoma, and third pair of setae inserted within the striated integument anterior to the OC. PD much smaller than in the female. Ventral plates separate. Genital plate lacking. Larva with three pairs of 5-segmented legs. Genu and tibia I each with a pair of spines but no ventral bristles.



Figs 1-10. Lobohalacarus weberi tristanensis subsp. nov., female; 1. idiosoma, dorsal; 2. idiosoma, ventral; 3. gnathosoma, lateral; 4. tarsus I, lateral (medial setae and claw omitted); 5. leg I, medial; 6. basifemur to tarsus II, medial; 7. basifemur to tarsus III, medial; 8. basifemur to tarsus IV, medial; 9. posterior tibia and tarsus II, medial (lateral claw omitted); 10. tarsus III, medial; 8. dorsal setae; 0. posterior dorsal plate; AE, anterior epimeral plate; ds, dorsal setae; ds(PE), dorsal seta on PE; ep, epimeral pore; gac, genital acetabula; 1m, lateral membrane; ls, lateral seta; OC, ocular plate; pas, parambulacral setae; pgs, perigenital setae; PD, posterior dorsal plate; PE, posterior epimeral plate; so, solenidion; vs, ventral seta)

VARIABILITY

Length of females 310-341 µm (with frontal spine included) or 301-314 µm (frontal spine excluded). The females proved to be highly variable in external characters. Three of the specimens have an elongate and spine-like anteromedian idiosomatic extension (Fig. 11), one specimen has a short and rounded frontal hood (Fig. 12), and in two of the females, the anterior idiosoma is rounded (Fig. 13). The number of perigenital setae varies from two to four setae and the number of genital acetabula from one to two on either side. In the majority of species, the PE have one dorsal, one lateral and one ventral seta, but the dorsal seta may be lacking (Fig. 12). Bilateral asymmetry in the leg chaetotaxy is fairly common, e.g., in four specimens both genua I have a pair of ventral spines; in one specimen both genua I bear a long and slender ventrolateral seta and a short ventromedial spine; another specimen has a pair of spines on the left genu but a ventromedial spine and a ventrolateral seta on the right genu. Tibiae II each bear one seta-like ventral bristle, and either one (1 specimen, unilaterally) or two wide and bipectinate bristles; tibiae III have one ventral seta-like bristle plus one (5 specimens) or two (1 specimen) wide and pectinate bristles; tibiae IV all have ventrally one setalike and two pectinate bristles. Tarsi III generally bear four dorsal setae (Fig. 10), though, in the holotype, one tarsus has no more than three dorsal setae. One specimen has a ventral seta on both tarsi III, the other five specimens demonstrate asymmetry with either one or no ventral setae.



Figs 11-13. Lobohalacarus weberi tristanensis subsp. nov., female, dorsal variants of idiosoma; 11. with frontal spine; 12. with frontal hood (idiosoma with left lateral seta on PE); 13. anteriorly rounded (idiosoma with lateral setae on PE). (Is, lateral seta) Scale bars = 50 μm.

REMARKS

The specimens from Inaccessible Island undoubtedly belong to the *Lobohalacarus weberi* complex, a group of closely allied species and subspecies with records from Europe, Asia, Africa, Australia, South and North America.

The specimens from Inaccessible are given the rank of a subspecies, viz., *Lobohalacarus weberi tristanensis*. The population demonstrates a much higher tendency to variability than found in the nominate form *L. weberi weberi* (Romijn and Viets) in Europe. Most remarkable is the anterior idiosoma, arch-like, with small rounded tip or with long spine-like projection. In contrast, specimens from Europe, as well as species and subspecies from other geographical regions, always have a spine-

like process. Telofemora III and tarsi IV have two and three dorsal but no ventral setae whereas in the European *L. w. weberi* these segments bear ventral setae.

GEOGRAPHICAL AND BIOLOGICAL SURVEY

The genus *Lobohalacarus* is world-wide in distribution. It includes species and subspecies which are closely allied and belong to a single natural complex, the *Lobohalacarus weberi* group. *L. weberi* was described on the basis of a specimen collected in The Netherlands (Romijn and Viets, 1924). The species proved to be widely distributed in Europe, Africa, North America and the Hawaiian Islands (Viets, 1950; Imamura, 1981; and unpublished records), generally inhabiting hypogean (hyporheic) and epigean waters fed by groundwater. *L. bucharensis* Jankovskaja, known from juveniles only, was found in groundwater in Middle Asia (Jankovskaja, 1967, 1972). *L. bunurong* Harvey is a hyporheic Australian species (Harvey, 1988), and *L. hummelincki* Viets was taken on the bank of a river in Venezuela (Viets, 1940). *L. processifer* (Walter) is known from a juvenile from a lake in the Andes, at 5000 m (Walter, 1919), and *L. weberi gotoensis* Imamura is a stygobiontic species from lava caves, Japan (Imamura, 1970). *L. weberi tristanensis* was collected from a small stream, together with the oribatid mite *Trimaloconothrus* sp. (Barber-James, in prep.). *Lobohalacarus* primarily inhabits subterranean waters and areas where hypogean waters meet

Lobohalacarus primarily inhabits subterranean waters and areas where hypogean waters meet the surface. Lobohalacarus w. weberi prefers darkness (unpublished experiments). The specimens generally live in constantly waterlogged substrates, but they are known to survive in moist sand, within the water-film, for more than a month (Teschner, 1961). L. w. weberi can withstand marine conditions for a couple of hours, and brackish water with a salinity of 20 or 10 ppt for about one or two to three weeks respectively (unpublished preliminary experiments with a population from northern Germany, from a pond with Sphagnun fed by groundwater). Lobohalacarus weberi is thought to be primarily parthenogenetic (Bartsch, 1981). The fecundity

Lobohalacarus weberi is thought to be primarily parthenogenetic (Bartsch, 1981). The fecundity is low, probably a single generation per year and no more than 10 eggs per female (Teschner, 1963). The eggs are carefully deposited in the substrate, e.g., sand (Teschner, 1963). They are not conspicuously thick-walled, but still they may be more tolerant to both desiccation and higher salinities than are adults.

MORPHOLOGICAL VARIANTS AND CHARACTERISTICS IN LOBOHALACARUS

Representatives of the genus *Lobohalacarus* are characterized by : Idiosoma with seven pairs of dorsal setae (adanal setae included, dorsal seta on PE excluded); genital sclerites with acetabula; palps four-segmented; third palpal segment with median spine; slender fourth palpal segment with three setae in the basal whorl; genu I nearly as long as telofemur or tibia I; tarsus I with three dorsal seta, dorsolateral solenidion, one ventromedial spinelet or seta, pair of ventral setae, and pair of apical parambulacral setae; lateral membrane of claw fossa enlarged.

Lobolialacarus differs from the majority of halacarids in having seven pairs of dorsal idiosomatic setae but no gland pores. All closely related marine and freshwater genera, and the majority of halacarid genera in general, have six pairs of dorsal setae and one to five pairs of gland pores. Five pairs are thought to be the original number of pores. The first pair of pores are almost always present, while the other pores may be greatly reduced, absent or replaced by setae. Substitution by setae is found in the majority of species of the genus *Rhombognathides* and *Metarhombognathus* (Bartsch, 1992), and in at least one species of *Lohmannella* (Bartsch, 1993). In species of the *L. weberi* complex, the anterior pair of setae is believed to correspond with the first pair of dorsal setae regularly present in

halacarid mites, whereas the pair of setae in the lateral margin of AD may originate from gland pores.

The author's halacarid collection includes more than a hundred specimens of *Lobohalacarus weberi*, from Europe (northern Baltic, northern Germany, Spain), northeastern America (Rhode Island), and the Hawaiian Archipelago; the specimens were collected from various substrates such as groundwater wells, ponds and small streams with mosses and pH as low as 4.5-5.0, and fine sand, more or less rich on organic material, pH-values of 6.0-7.8, and also slightly influenced by brackish water.

Variability was studied on populations from Europe and the United States, viz., 20 specimens each from two sites in Germany, and a small number of specimens from northern Baltic, Spain, Rhode Island (Table 1) and Hawaiian Islands.

Characters known to vary in Lobohalacarus are:

Frontal spine. The nominate species L. w. weberi always has a frontal spine.

Genital acetabula. The majority of subterranean living species have two pairs of genital acetabula whereas specimens from epigean waters, such as lakes, ditches, and habitats influenced by slightly brackish waters, have three pairs of genital acetabula. But, generally, within a population (sample) both variants are present, asymmetry is fairly common. In populations from northern Germany, 77-97 % of the specimens had genital sclerites with two acetabula. Specimens with a small, primordial acetabulum beside the one or two well developed genital acetabula are present, too.

Number of perigenital setae. The most common variant in European populations are five pgs on either side. About 15-25 % of the specimens in a given population, from both Europe and America, have four pairs of setae. The combinations 2/4 (two setae on one side, four setae on the other side), as well as 6/5 have been found in a population from Germany.

Genn I. The majority of specimens have the combination sp/br, that is ventromedially a spine and ventrolaterally a bristle. In the two populations from Northern Germany, 2-6 % had spines both ventromedially and ventrolaterally, asymmetrically or on both legs. Exceptionally, the spine or seta is lacking.

Tibia II. Most specimens have one ventral seta and two wide, pectinate ventromedial bristles. A single bipectinate bristle (aside from the ventral seta) is found in 0-20 % of the specimens in a given population. One specimen from the Northern Baltic had two pectinate bristles and two smooth and slender setae.

Tibia III. Most abundant are two ventral bristles, one short and bipectinate, the other longer, setalike and very faintly plumose. Though, in populations from northern Germany and northeast America, 30-40 % of the specimens had three ventral bristles, with two of them being wide and coarsely pectinate.

Tibia IV. They generally have three ventral bristles, one of them is seta-like and slender, two are wide and pectinate. Exceptions, viz., tibiae with two ventral bristles, one wide and pectinate, the other slender, seta-like and delicately plumose, are very rare.

Telofemnr III. The specimens from the northern Baltic and northern Germany all have the chaetotaxal combination 2/1 (two dorsal and one ventral setae), whereas specimens from Spain and from eastern America either had 2/1 or 2/0 setae.

Telofemmr IV. Both combinations 2/1 and 2/0 are commonly represented.

Tarsus III. Four dorsal and one ventral seta is the most common variant, other combinations are found, though only unilaterally.

Tarsus IV. Generally, 3/1 (three dorsal and one ventral) setae are present. The combination 3/0 has been found, unilaterally, in two specimens from northeastern America. Specimens with two ventral setae, instead of one, have been seen in European and northern American populations.

TABLE 1. Lobohalacarus weberi, variants of characters and, in brackets, percentage of variants in populations from: Northern Germany, population A (groundwater well), population B (bog with Sphagnum); Northern Baltic (muddy sand, brackish water); Rhode Island (riverines with Sphagnum); Inaccessible Island (river with Spartina).
(br = bristle; d/v = dorsal/ventral; sp = spine)

Populations from	Northern Germany A B		Northern Baltic	Rhode Island	Inaccessible Island
Character					
Anterior AD	spine (100)	spine (100)	spine (100)	spine (100)	spine (50) hood (17) rounded (33)
Number of	2 (97)	3 (19)	3 (71)	3 (5)	2 (83)
genital acetabula	1 1/2 (3)	2 1/2 (3) 2 (77)	2 (29)	2 (95)	1 (17)
Number of	5 (68)	6 (4)	5 (94)	5 (74)	4 (42)
perigenital setae	4 (26) 3 (6)	5 (77) 4 (15) 2 (4)	4 (6)	4 (26)	3 (42) 2 (16
I-4, combination of sp and br	sp/br(96) sp/sp (2) 0/br (2	sp/br (94) sp/sp (6)	sp/br (100)	sp/br (100)	sp/br (25) sp/sp (75)
II-5, number of pectinate bristles	2 (100)	2 (87) 1 (13)	2 (100)	2 (80) 1 (20)	2 (92) 1 (8)
II-5, number of pectinate bristles	1 (100)	1 (58) 2 (42)	2 (100)	1 (67) 2 (33)	1 (83) 2 (17)
IV-5, number of pectinate bristles	2 (92) 1 (8)	2 (100)	2 (100)	2 (100)	2 (83) 1 (17)
III-3, number of d/v setae	2/1 (100)	2/1 (100)	2/1 (100)	2/1 (90) 2/0 (10)	2/0 (100)
IV-3, number	2/1 (34)	2/1 (25)	2/1 (61)	2/1 (48)	2/0 (100)
of d/v setae	2/0 (66)	2/0 (75)	2/0 (39)	2/0 (52)	
III-6, number of d/v setae	4/1 (100)	4/1 (100)	4/1 (82) 3/2 (9) 2/1 (9)	4/1 (100)	4/1 (50) 4/0 (42) 3/1 (8)
IV-6, number of d/v setae	3/1 (97) 3/2 (3)	3/1 (100)	3/1 (100)	3/1 (90) 3/2 (5) 3/0 (5)	3/0 (100)

Basifemur IV. Both variants, with one or no ventral setae, are represented in the material studied.

The *Lobohalacarus weberi* complex includes species and subspecies which are extremely similar in their general facies. Descriptions and discrimination of *Lobohalacarus*, and halacarids in general, are based on external morphological characters. Ultrastructural investigations or data from karyological or molecular genetic studies are lacking until now. Studies in invertebrate taxonomy, using such techniques, proved a number of morphologically almost identical populations to represent complexes of subspecies or species (Grassle and Grassle, 1976; Pietsch and Westheide, 1985; Schlegel *et al.*, 1991; Wood and Backus, 1992; Schmidt and Westheide, 1994).

The external characters in the population of *Lobohalacarus weberi* on Inaccessible Island show some overlap with those of *L. weberi* from the northern hemisphere. Differences in the leg chaetotaxy, the unusual high degree of variability in the Inaccessible population, the geographical distance between northern Europe (with *L. weberi weberi*) and the South Atlantic island in view of low dispersal ability of *Lobohalacarus*, are reasons to distinguish between the populations and to give the specimens from Inaccessible Island the rank of a separate subspecies.

DISPERSAL AND COLONIZATION OF OCEAN ISLANDS

Because of the subsurface way of life and wide geographical distribution of the *Lobohalacarus weberi* complex (records exist from all continents except for Antarctica which has not been studied), one may speculate that these freshwater halacarids belong to an ancient taxon which had already invaded the freshwater of the supercontinent Pangea (Bartsch, 1982). However, the Tristan da Cunha island group and the Hawaiian Islands, both of which have records of *Lobohalacarus*, are of more recent origin. Multiple invasion of a formerly marine ancestor and subsequent speciation and adaption to fresh water is unlikely; thus, *Lobohalacarus* must have been transported to these islands.

Marine, brackish as well as terrestrial species can be spread over long distances through rafting, but *Lobohalacarus*, unable to live but a few hours in seawater, would certainly not survive a transport, drenched with seawater and salt spray, to a distant oceanic island. As documented by Maguire (1963), small aquatic organisms can be dispersed by large animals. *Lobohalacarus weberi*, which can survive in a moist substrate for weeks (Teschner, 1961), may have colonized Inaccessible Island via air, attached to birds or insects which visited continental wells, banks of rivers or groundwater-fed epigean ponds and later rested on Inaccessible Island.

Recent geological investigations by Christie *et al.* (1992) showed that seamounts along submarine ridges once had been islands raised above sea level. These eroded and drowned islands, being considerably older than the present-day volcanic islands in the Galapagos and Hawaiian archipelago, may have been stepping stones for the biota now found on these archipelagos (Christie *et al.*, 1992; Carson, 1992). It is tempting to suppose that the Walvis Ridge provided similar stepping stones and thus eased the colonization of Inaccessible Island.

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